

## EVOLUTION OF THE TELSON NEUROMUSCULATURE IN DECAPOD CRUSTACEA

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### ABSTRACT

The neuromusculature in the telsons of three macrurans (*Pandalus platycernus*, *Procambarus clarkii*, *Upogebia pugettensis*) and three anomurans (*Munida quadrispina*, *Blepharipoda occidentalis*, *Emerita analoga*) are compared to provide a framework for neurophysiological comparisons of their roles in the swimming behaviors of these decapods. The stereotypical arrangement in macruran telsons comprises a group of massive axial muscles and a trio of small appendage muscles (Fig. 1). The various arrangements of telson neuromusculature in the anomurans (Fig. 3) are interpreted in terms of specific modifications of particular macruran features. Homologies among muscles and nerve roots in the telsons of the six decapods are identified (Figs. 1, 3, 4, Table II) and homologies among particular axial and appendage motoneurons in the sixth abdominal ganglia are suggested (Fig. 5, Table III). The appendage neuromusculature in decapod telsons is inferred to be ontophyletically part of the seventh abdominal segment that was present in the ancestors of decapods. These muscles and their motoneurons, like most of the axial neuromusculature in the telson (Dumont and Wine, 1983, in prep.), may be serial homologs of muscles and motoneurons in abdominal segments.

### INTRODUCTION

Phylogenetic histories of neuronal circuits could contribute to neurobiology by revealing what features of neurons and neural circuits respond to selective pressures by evolving new behaviors and what features are conserved through evolution. The neural control of the decapod crustacean tailfan is particularly well suited for such a phylogenetic analysis. This is because the tailfan is an ancestral structure in decapods. It contributes to tailflipping locomotory behaviors that are already subjects of intensive neurobiological investigations in the crayfish, a macruran, and it has been modified in several anomuran families for use in other behaviors.

The tailfan is a tripartite structure comprised of the telson flanked by the paired appendages of the last abdominal segment, the uropods. Paleontological and embryological observations indicate that the tailfan is an ancestral decapod structure that is present during some part of the life cycle in all decapods. The fossil record documents its long history from the Paleozoic Era (Schram, 1982); the fossilized abdomen and tailfan of the "first decapod," *Paleopalaemon newberryi*, is very similar to that of modern reptant macrurans (Schram *et al.*, 1978). Since the Paleozoic, the tailfan has been structurally and functionally modified to perform new behaviors in several

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*Abbreviations.* Muscles: AT, anterior telson; ATU, anterior telson-uropodalis; DR, dorsal rotator; F6, terminal component of fast flexors in segment 6; LTU, lateral telson-uropodalis; PTF, posterior telson flexor; PTU, posterior telson-uropodalis; Re, uropod remotor; RS, uropod return-stroke; STF, slow telson flexor; TU, telson-uropodalis muscles; VR, ventral rotator; VTF, ventral telson flexor.

anomuran families descended from macrurous decapods (see *e.g.*, Chapple, 1966, 1977; Paul, 1981a, b), so that a wealth of comparative material is potentially available to allow verification of conservation of features (among macrurans and unchanged parts of anomurans) against which newly evolved anomuran features can be recognized.

Most investigations of the macruran tailfan have been done on crayfish. They have concerned its role in different forms of tailflipping (Wine and Krasne, 1982), activation of some of the telson muscles in these different behaviors (Kramer *et al.*, 1981a; Kramer and Krasne, 1984), the relationship of telson musculature to the fast flexor neuromusculature of the abdomen (Larimer and Kennedy, 1969a, b; Dumont and Wine, 1983, in prep.), the integration of sensory input (Wilkens and Larimer, 1972; Calabrese, 1976; Wiese, 1976), and the addition of mechanoreceptive hairs and neurons to the tailfan during adult growth (Letourneau, 1976). Recently, some of the motoneurons, local interneurons, and projection interneurons in the terminal abdominal ganglion have been described (Takahata *et al.*, 1981; Reichert *et al.*, 1982; Sigvardt *et al.*, 1982; Dumont and Wine, 1983, in prep.; Nagayama *et al.*, 1983). It has been difficult to integrate neurobiological investigations on the tailfans of other decapods with these crayfish studies because the organizational plan of the telson neuromusculature has not been fully described. Published treatises on the musculature of macrurans (Schmidt, 1915; Berkeley, 1927; Daniel, 1931; Young, 1959) are detailed but predate the modern neurobiologist's functional perspective, and they do not include innervation of individual muscles. Larimer and Kennedy (1969a) began to rectify this for the crayfish from the perspective of differentiation of neuromusculature into phasic and tonic systems. But the arrangements of muscles and nerves in the tailfans of some other decapods appear, at least superficially, very different from crayfish.

We have compared the tailfans in representatives of six families (Table I) to find out whether there is a fundamental plan of organization that describes the musculature in all decapod telsons. We conclude that, even though the telson is not a somite and has no appendages of its own, the telson neuromusculature is divisible into axial and appendage systems, each with entirely separate innervation. And within these two groups, individual muscles and their motoneurons can be recognized and compared among families. Thus, the various arrangements of muscles in the different anomuran telsons can be understood in terms of specific modifications of particular features in the basic macruran plan. Our results provide the necessary ground work for the identification of homologies among the motoneurons serving the tailfan in different decapod groups and for rigorous testing of hypotheses regarding the evolution of neural circuits mediating new behaviors (Paul, 1979, 1981a, b).

#### MATERIALS AND METHODS

*Procambarus clarkii* were obtained from Beachcomber Biological, Oakland, California, and held in continuously flowing freshwater aquaria. Prawns, *Pandalus platycoccus*, squat lobsters, *Munida quadrispina*, and mud shrimps, *Upogebia pugettensis*, were collected locally. Sand crabs, *Blepharipoda occidentalis* and *Emerita analoga*, were collected from Monterey Bay, California. The marine animals were maintained in aquaria in a recycling, 10°C sea water system.

Anatomical investigations were made on freshly dissected specimens. The animals were anaesthetized by chilling before severing the abdomen from the thorax. Most dissections were made from the ventral side, but dorsal and sagittal perspectives of the internal anatomy of segment 6 and the telson were obtained, by the appropriate dissections, to verify the relative positions of muscles and nerves as described from

the ventral approach. Diagrammatic drawings of the features of interest were made with the aid of a camera lucida mounted on a Wild M5 stereomicroscope. Our anatomical descriptions are based on dissections and drawings of a minimum of ten specimens of each species.

Innervation from the terminal (sixth) abdominal ganglion of tailfan neuromusculature and sensory fields was traced by staining freshly dissected tailfans with methylene blue and by electrophysiological methods. We used suction electrodes to stimulate and record from individual nerves to verify that they innervated particular muscles or contained afferents from sensory hairs on the exoskeleton as shown by the staining. Muscle responses were noted by observing contractions under low power magnification of a stereomicroscope, or by recording electrical responses via small suction electrodes or 20 Megohm KCl-filled microelectrodes in muscle fibers. Conventional methods were used to amplify and display the signals on an oscilloscope (Paul, 1971b).

The number of motoneurons in selected nerves, positions of their somata, and the morphology of their principal neurites in the ganglion were revealed by immersing the cut nerve end in 250 mM NiCl<sub>2</sub> at 4°C for 4–18 hours, followed by precipitation of the Ni<sup>2+</sup> with dithiooximide (rubeanic acid; Quicke and Brace, 1979). The stain in some ganglia was intensified with silver (Bacon and Altman, 1977). All ganglia were processed conventionally (Paul, 1981b) and viewed at 160–250× magnification with a Zeiss compound microscope that was equipped with camera lucida. Nerves of interest were backfilled repeatedly (10–20 times) in each species until we were confident, within the limitations of the backfilling technique, that the largest number of motoneurons that we filled (observation repeated in at least three specimens) was the actual number of motoneurons in the nerve.

## RESULTS

The crustacean body terminates in the telson, which thus articulates with the last true segment (abdominal segment 6 in decapods). The telson is flanked by uropods, the paired appendages of segment 6, and together with them forms a tripartite structure called the tailfan. Elsewhere in the body, skeletal muscles are readily subdivided into appendages (arising in the trunk and inserting on an appendage) or axial (arising and inserting along the body trunk), but in the telson of macrurans, such as crayfish, the organization of muscles appears complex, and functional divisions are difficult to understand. We first describe the arrangement in the macruran telson based on examination of members of three families (Table I), and show that a division between axial and appendage muscles also exists. We then consider the organization of the telson neuromusculature in three anomurans (Table I) with modified tailfans. Finally,

TABLE I

*Decapods of the suborder Pleocyemata used in this study (classification to family according to Bowman and Abele, 1982)*

Infraorder	Family	Genus, species
Caridea	Pandalidae	<i>Pandalus platycerus</i> Brandt
Astacidea	Astacidae	<i>Procambarus clarkii</i> Girard
Thalassidea	Upogebidae	<i>Upogebia pugettensis</i> Dana
Anomura	Galatheididae	<i>Munida quadrispina</i> Benedict
	Albuneidae	<i>Blepharipoda occidentalis</i> Randall
	Hippidae	<i>Emerita analoga</i> Stimpson

we interpret the arrangements in these anomuran telsons in terms of specific modifications of particular features of the ancestral macruran plan.

### *Macruran telson*

We use the crayfish as our 'type specimen' for macruran tailfans for several reasons. Precedence: published descriptions of tailfan neuromusculature are more complete for crayfish than for any other macruran (Schmidt, 1915; Larimer and Kennedy, 1969a). Crayfish have been used much more frequently for neurophysiological studies than other macrurans, so that a nomenclature for the nerves and muscles is becoming established (Larimer and Kennedy, 1969a; Kramer *et al.*, 1981a, b; Wine and Krasne, 1982; Dumont and Wine, 1983; Kramer and Krasne, 1984). Finally, we have concluded from our work with crayfish, other macrurans, and anomurans (this study; Paul, 1981b) that the crayfish plan and nomenclature are applicable to the neuromusculature in the telsons of other decapods.

*Axial muscles.* The apparent complexity in functional arrangement of the seven telson muscles in crayfish stems from the fact that four of them insert on one tendon that is continuous with the caudal-most component of the anterior-oblique, fast flexor muscles in segment 6. Near the caudal end of segment 6, this flexor tendon is focally attached to the tendon of the ventral rotator muscle at a point antero-medial to the rotator's insertion on the uropod propodite (Fig. 1A<sub>1</sub>). It is also bound to the partial arthrodistal membrane between segment 6 and telson, through which it passes, so that the three components of the tailfan are mechanically coupled to each other. Three of the telson flexor muscles [the ventral, slow, and posterior telson flexor (ventral head), VTF, STF, and PTF] arise from the ventral cuticular membrane, whereas two muscles (the rest of PTF and the anterior telson muscle, AT) arise from the inner dorsal surface of the telson (Fig. 1A; Fig. 2A). This means that the force vector generated by contraction of any one of the six muscles that share the tendon must depend on the degree of activity in the other muscles. All four of these telson muscles are part of the axial musculature by the criteria of their shared tendon with the fast flexor muscles in segment 6, and by their innervation through root 6 (see below) by motoneurons that, with one exception, are the homologs in G6 of flexor motoneurons in more rostral ganglia (Dumont and Wine, 1983). The VTF, PTF, and AT muscles are active during non-giant mediated tailflips (Kramer and Krasne, 1984); VTF and PTF continue the line of axial flexors down the ventral side of the animal (Figs. 1A<sub>1</sub>, 2) and contribute to flexion of the telson. The AT muscle is the single exception to the clear division between axial and appendage musculature. It inserts on the dorsal side of the flexor tendon (Fig. 2) and not directly on the uropod propodite but, because of its nearly vertical orientation and the tight mechanical linkage between tendons and arthrodistal membranes on the ventral side at the juncture of telson, uropods, and segment 6, this 'axial' muscle pronates the uropod and makes no contribution to flexion of the axis (Dumont and Wine, in prep.). The AT muscle (ATF in Larimer and Kennedy, 1969a) is anomalous in another respect for it has no homolog in the abdominal segments, nor is its single motoneuron homologous to any of the rostral flexor motoneurons (Dumont and Wine, in prep.; see Discussion).

*Appendage muscles.* The remaining muscles in the telson, the telson-uropodalis (TU) muscles (anterior, posterior, and lateral; ATU, PTU, and LTU), arise from a common tendon attached to the dorsal surface of the telson at a point slightly lateral and caudal to the origin of AT (Fig. 1A). They diverge before their insertions on the uropod, PTU and LTU close together on the inner ventral surface of the propodite and ATU on its medial, rostral rim, adjacent to the insertion of the dorsal rotator

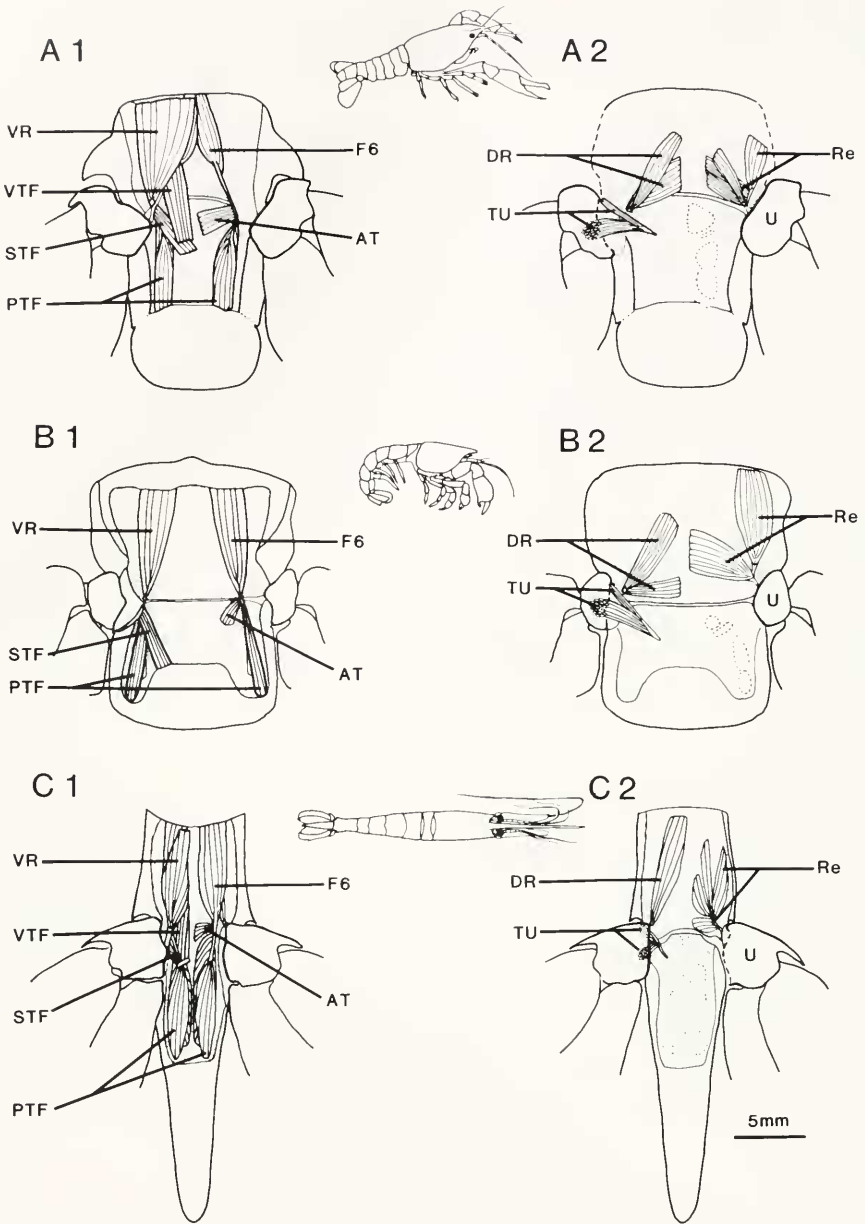


FIGURE 1. Macrurans: ventral aspects of the sixth abdominal segment and tailfan dissected to show all of the telson muscles and those muscles in segment 6 that insert on the uropod. Anterior towards the top. A: *Procambarus*; B: *Upogebia*; C: *Pandalus*. A<sub>1</sub>, B<sub>1</sub>, C<sub>1</sub>: axial muscles. A<sub>2</sub>, B<sub>2</sub>, C<sub>2</sub>: appendage muscles that insert ventrally (left side of each figure) and dorsally (right side of each figure) on the uropod propodite (U). Areas enclosed by dotted lines, origins of muscles (axial and appendages) on inner dorsal surface of telson.

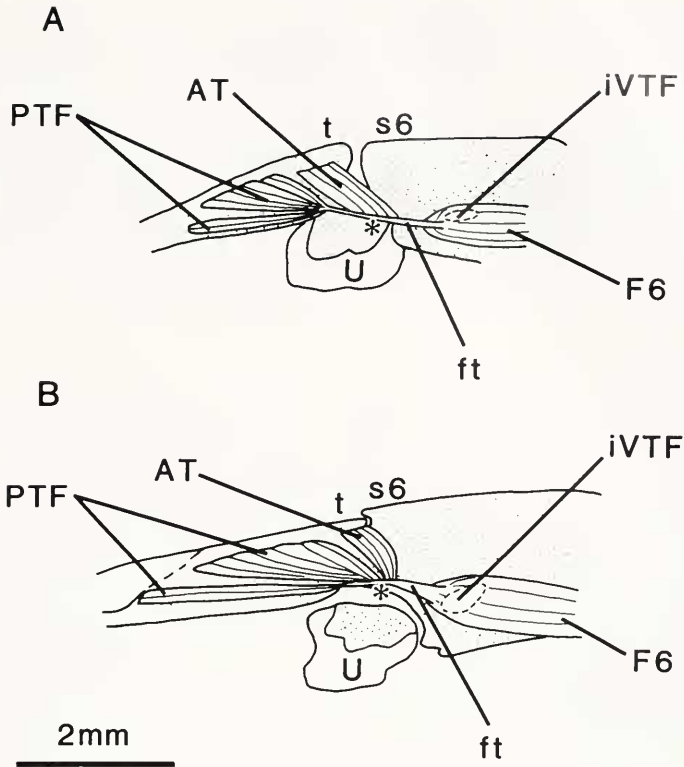


FIGURE 2. Sagittal view of left side of telson (t), segment 6 (s6), and medial edge of left uropod propodite (U) in A, *Procambarus* and B, *Pandalus* to show the flexor tendon (ft) that in macrurans interconnects the axial muscles in the telson and s6. iVTF, insertion of VTF on F6 muscle; \*, approximate location of the interconnection between the ft and the more lateral, perpendicularly oriented TU tendon (see Fig. 1 and text).

muscle. The TU muscles are very small compared to the massive telson flexor muscles. Their actions would appear to be depression of the uropod (see also Larimer and Kennedy, 1969a). The TU tendon is mechanically linked by strong connective tissue to both the arthrodial membrane in the plane between sixth segment and telson and to the longitudinally oriented flexor tendon (Figs. 1, 2); this would appear to severely limit the TU muscle's independence from the axial musculature.

#### *Is the crayfish plan general for macrurans?*

Macrurans comprise two subgroups, the Reptantia or "crawlers," with abdomen flattened dorso-ventrally, and the Natantia or "swimmers," with abdomen flattened laterally. *Upogebia*, like crayfish, is a reptantian. Its telson muscles are virtually identical to those in crayfish with the exception that VTF is absent (Fig. 1B). The telson of natantians, such as *Pandalus*, is narrower and the uropods more ventral than in Reptantia, but the four axial muscles in the telson are arranged as in crayfish (Figs. 1, 2). The TU muscles are also present and arise from a long, slim tendon that bifurcates to attach to the anterior-dorsal telson, lateral to the origin of AT, and to the posterior-dorsal margin of segment 6, and in mid-course to the arthrodial membrane and flexor tendon, as in Reptantia. The TU muscles are shorter, however, because

they arise ventral to the PTF muscle; they extend ventrally to insert on the inner surface of the propodite in positions somewhat more lateral than their homologs in crayfish (Fig. 1C<sub>2</sub>).

Although the Reptantia-Natantia division is not taxonomically valid (Schram, 1982), it recognizes the association between two body forms and two modes of living, primarily benthic and primarily pelagic, and is therefore functionally useful. Indeed, the similarity in internal organization despite disparate external form between macruran telsons (compare A and C, Fig. 1) highlights the internal modifications of the ancestral macruran plan in anomuran telsons that externally resemble those of reptant macrurans (see below; compare Fig. 3A, B with Fig. 1A, B; Paul, 1981b).

### *Anomuran telsons*

*Axial muscles.* The number of muscles in the flexor system is smaller in Anomura than in macrurans. Nevertheless, the homology of individual muscles with specific telson flexors in crayfish can be recognized on the basis of relative positions, origin, and innervation by the homolog of crayfish's R6, supplemented by positions and morphologies within the ganglion of the motoneurons innervating each muscle (Fig. 3A-C; see *Innervation*, also Chapple, 1977; Mittenthal and Wine, 1978; Paul, 1981b).

The PTF is the most robust axial muscle in all the decapods. In *Munida* and *Blepharipoda*, it retains its role in telson flexion; but in *Emerita* it inserts directly on the uropod propodite and its sole action is to pronate (and protract) the uropod; it has become functionally an appendage rather than an axial muscle (Fig. 3C, Table II; Paul, 1981b). *Emerita's* PTF (=VM) muscle has been erroneously homologized with the sixth segment ventral rotator muscle in the Galatheid *Galathea strigosa* (Maitland *et al.*, 1982). [This paper also misnamed the dorsal rotator muscle (MR in *Emerita*) that occurs in both macrurans and anomurans (Figs. 1, 3) as the medial remotor; the remotor muscles, as their name implies, insert on the dorsal, not the ventral side of the propodite (Figs. 1, 3).] The STF muscle is reduced in size and innervation in all of the anomurans (Fig. 3; Table III). The VTF is absent, as it is in some macrurans (Fig. 1B), and so is the AT muscle. The loss of AT in the Anomura was probably related to the greater mobility of their uropods: in crayfish the AT muscle contributes to cupping of the uropods (Dumont and Wine, in prep.), a function that has been taken over by a muscle that inserts directly on the propodite, the ATU muscle.

*Appendage muscles.* In contrast to the simplification of the axial muscles, the appendage (TU) muscles in the telson of the anomurans have become enlarged compared to their homologs in macrurans (Figs. 3A-C). TU muscle fibers arise directly from the inner dorsal surface of the telson over rather broad areas (Fig. 1A<sub>2</sub>-C<sub>2</sub>). Three separate heads are recognizable in *Munida* and *Blepharipoda* by their slightly different orientations (origins and insertions) (Fig. 3A<sub>2</sub>, B<sub>2</sub>); they have been called the coxopodite adductor muscle (ATU + PTU) and the accessory coxopodite adductor (LTU) in *Galathea strigosa* (Maitland *et al.*, 1982). In *Emerita* the three TU muscles have become functionally specialized into the dorsomedial, the power-stroke, and the lateral muscles (Paul, 1971b, 1981b) which we think are the respective homologs of ATU, PTU, and LTU in crayfish (Fig. 3C). The ATU muscle in all three anomurans strongly resembles part of the macruran axial musculature, the AT muscle, in its origin (antero-dorso-medial telson), its orientation, and, to a lesser extent, the approximate position of its insertion (respectively, on and close to the medial ventral rim of the propodite): compare ATU in Figure 3A-C with AT in Figure 1A-C. We

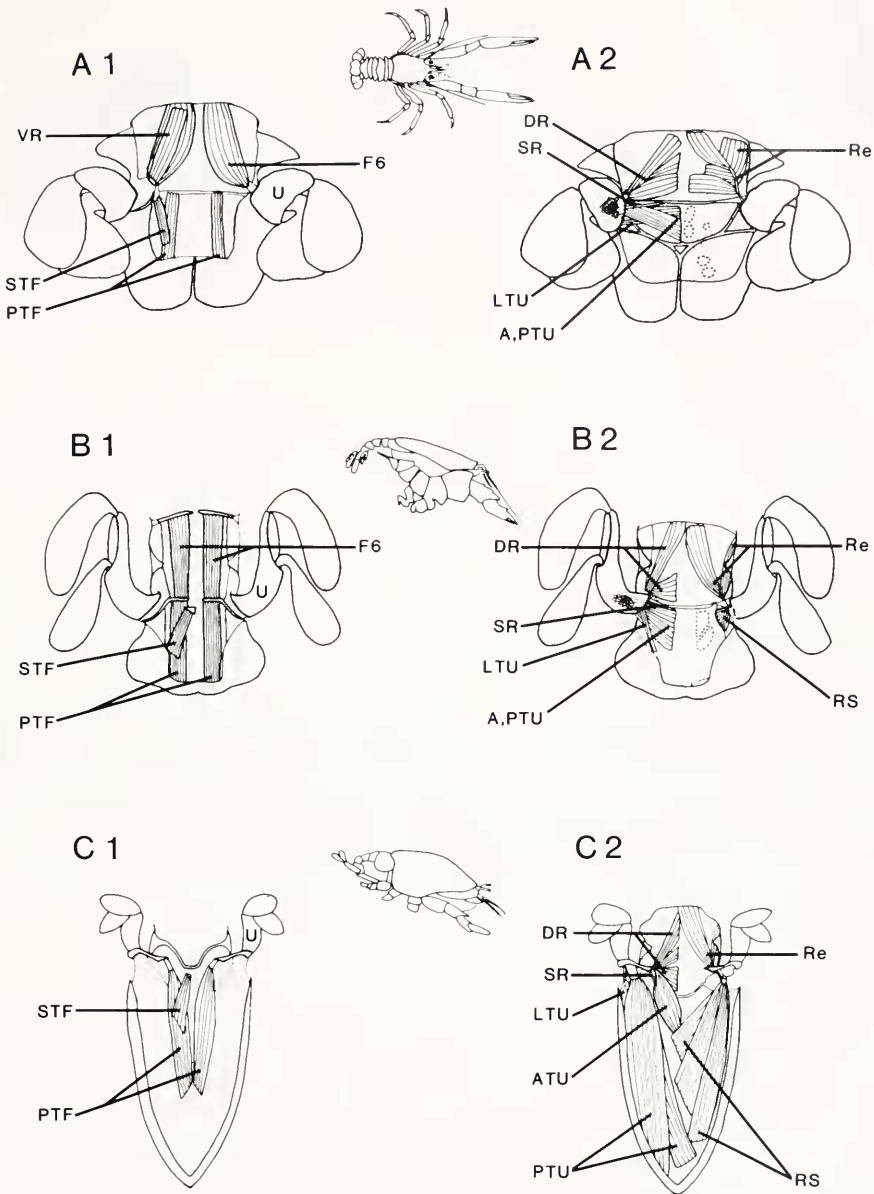


FIGURE 3. Anomurans: ventral aspects of sixth abdominal segment and tailfan to show muscles in telson and segment 6 of A, *Munida*, B, *Blepharipoda*, C, *Emerita*. Layout, scale, and abbreviations the same as for Figure 1. (B, C modified from Paul, 1981b). The dorsal surface of the telson of *Munida* is composed of plates separated by unsclerotized arthrodial membrane. Two heads of the PTF muscle arise from the caudal plate. The stretch receptors (SR) in A and B are shown in their correct position but actually would be partially hidden by ATU in this perspective. Alternate names in galatheids (from Maitland *et al.*, 1982) and in sand crabs (Paul, 1971b, 1981b): ATU: galatheid coxopodite adductor, sand crab dorsomedial muscle (DM); DR: sand crab medial rotator (MR); LTU: galatheid accessory coxopodite adductor, sand crab lateral muscle (LA); PTF: sand crab ventromedial muscle (VM); STF: sand crab medial muscle (ME); VR: in part, galatheid uropod-telson flexor.



TABLE II

*Telson muscles*

	Axial				Appendage		Stretch receptor
	VTF	AT	STF	PTF	TU	RS	
<i>Procambarus</i>	+	+	+	+	+	-	-
<i>Pandalus</i>	+	+	+	+	+	-	-
<i>Upogebia</i>	-	+	+	+	+	-	-
<i>Munida</i>	-	-	+	+	+	-	+
<i>Blepharipoda</i>	-	-	+	+	+	+	+
<i>Emerita</i>	-	-	+	+	+	+	+

were, in fact, misled by this strong anatomical resemblance into considering the ATU in anomurans to be the homolog of the macruran AT muscle until we had investigated their innervations (see *Innervation*; Figs. 4, 5).

*Comparison between telson musculature in macrurans and anomurans*

The muscles present in the telsons of the six animals are summarized in Table II. In the order listed, there is a decrease in number and in size (relative to size of tailfan) of individual axial muscles. The anomurans have done away with the flexor tendon between the axial muscles in the telson and segment 6. *Munida* and *Blepharipoda* have lightly sclerotized and quite flexible telsons, so that their axial muscles both bend the telson and flex it on the abdomen. In *Emerita* the principle axial muscle, PTF, is retained even though the hinge between segment 6 and telson is nearly immobile, but it inserts directly on the uropod and is active during the power stroke of this appendage (Table II; Paul, 1979, 1981b).

The TU muscles in anomurans are much larger than in macrurans. They all arise directly from the dorsal telson, each muscle from a different area (Fig. 3), in contrast to their origin from one tendon in macrurans (Fig. 1). Their insertions on the propodite are in roughly similar relative positions in all six animals.

TABLE III

*Motoneurons in R6 of G6*

<i>Procambarus</i> <sup>1</sup>	<i>Upogebia</i>	<i>Munida</i>	<i>Blepharipoda</i>	<i>Emerita</i>
Muscle:			predicted numbers	
VTF 5(2FF + 2FI + MoG)	0	0	0	0
AT 1	1	0	0	0
STF 4	4	4	4	≤4
PTF 7(4FF + 2FI + MoG)	7	6	6	6
total = 15 <sup>1</sup> Expect:	12	10	10	≤10
Found:	12	~8	8 <sup>3</sup>	6 <sup>2,3</sup>

<sup>1</sup> Physiological identifications of motoneurons in *Procambarus* from Larimer and Kennedy (1969) and Dumont and Wine (in prep.). FF, fast flexor motoneurons; FI, flexor inhibitor—both are shared by VTF and PTF; MoG, motor giant.

<sup>2</sup> Paul (1971b).

<sup>3</sup> Paul (1981b).

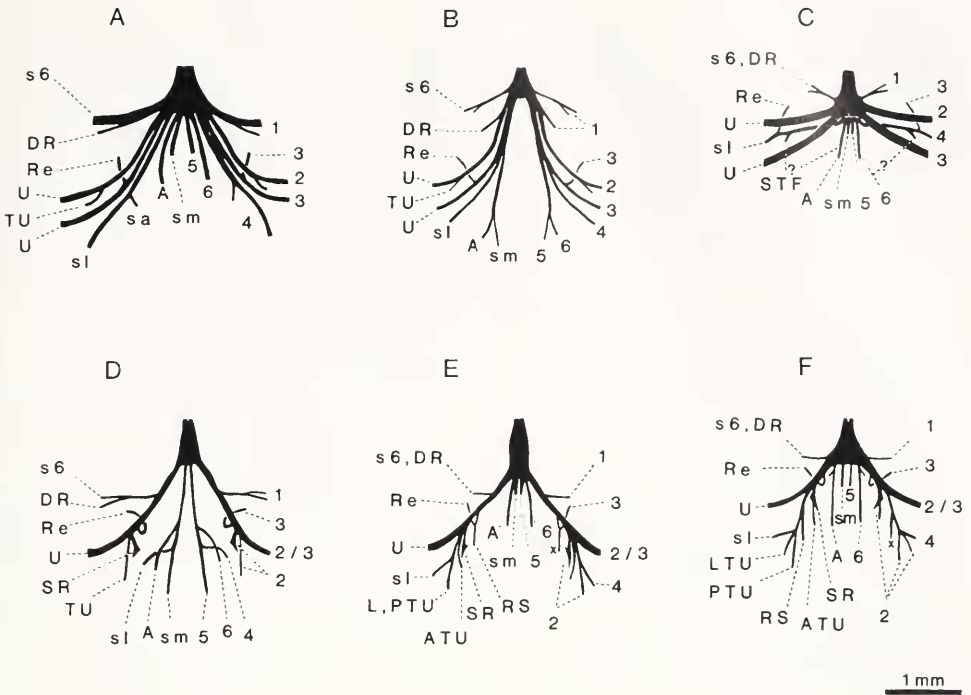


FIGURE 4. The terminal abdominal ganglion, G6, in A, *Procambarus*, B, *Upogebia*, C, *Pandalus*, D, *Munida*, E, *Blepharipoda*, F, *Emerita*. The ganglionic roots on the left side are labelled by the target they innervate, and on the right side by number according to their homology with roots in *Procambarus*: in D-F, roots 2 and 3 actually enter uropod as separate nerves as they do in macrurans. A, axial muscles (see Table II for muscles present in each species); field of sensory roots: s6, lateral and dorsal surfaces of segment 6; sa, sl, sm, anterodorsal, lateral, medioposterior telson, respectively; \* (E, F), RS nerve = ontophylogenically a branch of R3 (see Discussion). Ganglia, not roots, are drawn to the same scale—some of the roots are shown enlarged and spread apart for clarity.

Two additional features are included in Table II. First, to complete the list of telson muscles, is the return-stroke muscle (RS), peculiar to sand crabs (Fig. 3Bii, Cii). This "new" component of the appendage neuromusculature in the telson is the antagonist of the TU muscles, since its action is to elevate (and in *Emerita*, remote) the uropod (Paul, 1971b, 1981b). And finally, in the Anomura, a stretch receptor (SR) spans the basal joint of the uropod from anterior, dorsal telson to ventral, medial rim of the propodite (Fig. 3). It is closely allied with the ATU muscle (this study; Paul, 1971c, 1972) and its few muscle fibers and sensory neurons with central somata may have been derived from this part of the appendage neuromusculature. The receptor in galatheids was first reported in *Galathea strigosa* by Maitland *et al.* (1982), who incorrectly described the position of its dorsal attachment as in the middle of segment 6, rather than at the anterior edge of the telson; their illustration shows it to be in the same location as the SR in *Munida* (Fig. 3A<sub>2</sub>).

#### *Innervation of the telson*

*The sixth abdominal ganglion.* The terminal ganglion in decapods is fused embryonically from primordial abdominal ganglia six and seven, plus a terminal cell

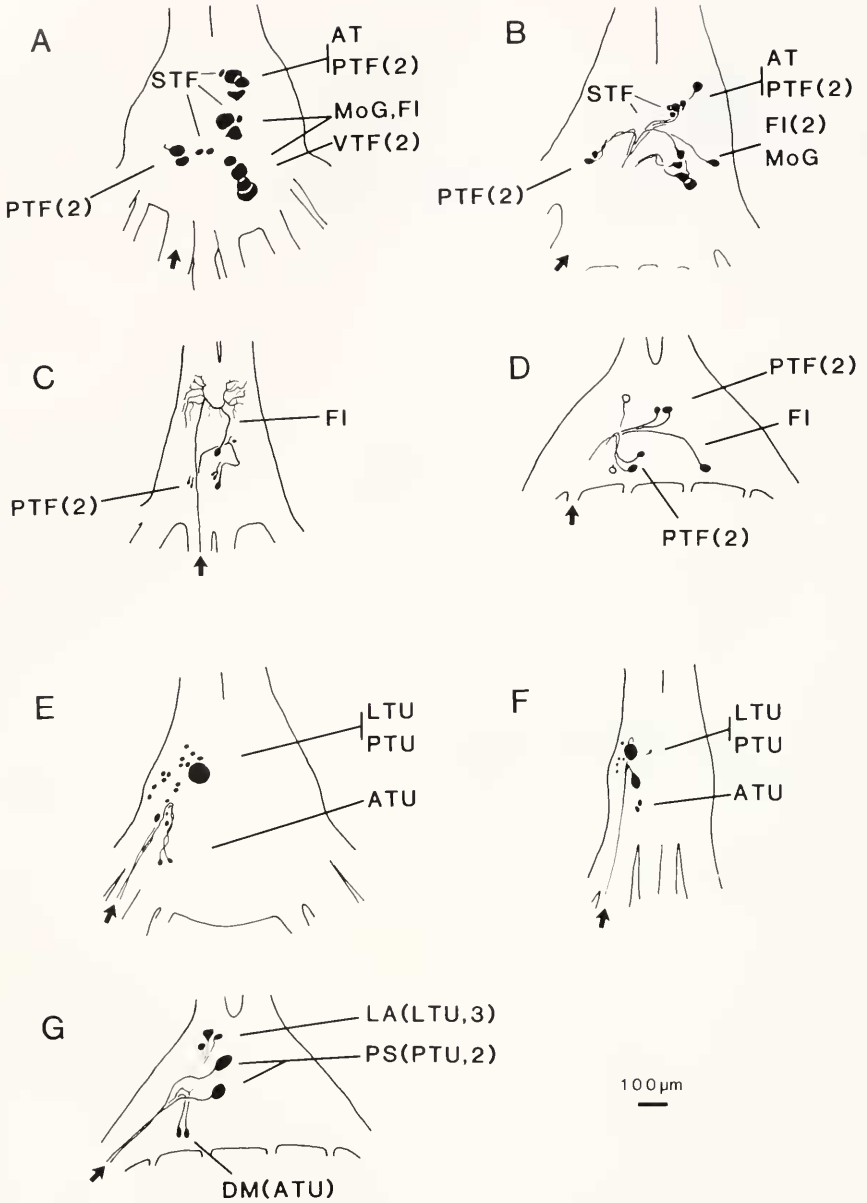


FIGURE 5. Motoneurons in G6 with (A–D) axons in R6 that innervate the axial muscles (see Table III) and (E–G) axons in R2 that innervate the appendage muscles in the telson. Anterior toward top of page. A, E, *Procambarus*; B, *Upogebia*; C, F, *Munida*; D, G, *Emerita*. Identification of fast flexor motoneurons in crayfish from Dumont and Wine (in prep.). Some of the R6 motoneurons in the other species are labelled by the similarities in their soma positions and neurite structures (not shown) with those of the identified crayfish motoneurons, but these identifications have not been confirmed physiologically. The open somas in D show the two alternate positions occupied in different specimens by one motoneuron (probably the STF motoneuron); the positions of the other five are invariant. R2 motoneurons are labelled from backfills of individual nervelets to the three muscles in *Emerita* (G; see Paul, 1981b) and their putative homologs suggested for crayfish (E) and *Munida* (F). The representative backfills shown for crayfish's and *Munida*'s TU branch of R2 may not include all of the smaller neurons. The SR somas are not included in F and G (see Paul, 1972; Maitland *et al.*, 1982).

cluster (Bullock and Horridge, 1965; Dumont and Wine, in prep.). It is the sixth free ganglion (G6) in the abdomen of macrurans. In the three anomurans we have studied, and also in pagurid anomurans (Chapple, 1977), the terminal ganglion is the fifth free ganglion, because abdominal ganglion 1 has fused with the last thoracic ganglion. Further condensation of the anterior abdominal nervous system has occurred in some other Anomura, further reducing the number of free ganglia in the abdomen (Bullock and Horridge, 1965). But, the terminal ganglion in all species is the homolog of the macruran G6 and, to facilitate inter-specific comparisons, we advocate that it and the other abdominal ganglia be numbered according to the number of their homologs in the uncondensed decapod nerve cord (see Paul, 1979).

*Nerve roots of ganglion 6.* The innervation of the axial and the appendage muscles is from two separate roots of G6. Because the number and positions of the nerve trunks leaving the ganglion are different in each species, we have adopted the numbering system for the roots in crayfish to describe the neuroanatomy of the other tailfans in order to facilitate inter-specific comparisons (Paul *et al.*, 1983, Fig. 4). Figure 4A shows the six roots that innervate the skeletal muscles of the crayfish tailfan (the 7th root, to the gut, is omitted); their destinations are given in the figure and legend (see also Larimer and Kennedy, 1969a). In the other macrurans and in anomurans some of the roots emerge from G6 as single trunks, giving the appearance of fewer than six ganglionic nerves. However, the distributions of the various branches to their final destinations (determined by methylene blue staining and electrical stimulation and recording from individual nerve branches; see Materials and Methods) reveal which are the roots corresponding to crayfish's. We have numbered them accordingly in Figure 4B-F.

*Innervation of telson muscles.* The arrangement of musculature in macruran tailfans is sufficiently uniform to present little problem in making interfamilial comparisons (Fig. 1), although their ganglionic roots are rather different (Fig. 4A-C). But anomuran tailfans have diversified so much that gross anatomical observation is inadequate to suggest homologies between individual telson muscles and their counterparts in macrurans (Paul, 1971b). In these cases innervation provided the clue to recognizing the subdivision between axial muscles, innervated by R6, and TU muscles, innervated by R2 (Fig. 4). And within each group, axial and appendage, the motoneurons serving individual muscles can be identified by backfilling with dye their individual nerve branches (Fig. 5). Homologs in the different families can then be suggested based on similarities in position and morphology of the motoneurons (Fig. 5; Paul, 1981b; see also: Chapple, 1977; Mittenthal and Wine, 1978; Sillar and Heitler, 1982). We have used this approach to examine the innervation of the axial muscles in the telsons of five of these decapods (all but the prawn).

The results of unilateral Ni-backfills of R6 in each animal are summarized in Table III (see also Paul *et al.*, 1983). On the left are listed the four muscles in *Procambarus*, followed by the number of motoneurons innervating each; the physiological identifications of motoneurons given in parentheses are from Larimer and Kennedy (1969a) and Dumont and Wine (in prep.). To investigate whether muscles and their motoneurons might be retained or lost together during evolution, we have compared the expected and actual number of motoneurons in R6 for each of the four genera. In *Upogebia* we found three fewer motoneurons than in *Procambarus*, as expected by the loss of the VTF with its two fast flexor motoneurons and one motor giant (both flexor inhibitors are shared with PTF and so would be expected to be retained). In the three anomurans we expected a reduction in numbers of R6 neurons greater than predicted by loss of the VTF and AT muscles (3 excitatory and 1 motor giant motoneurons) because none of these animals has giant interneurons

(Paul, 1971a; Paul and Then, unpub.), and we predicted that none would have the remaining motor giant, reducing PTF's innervation by one motoneuron. There are, in fact, even fewer R6 motoneurons than predicted. We attribute the discrepancy in *Munida* and *Blepharipoda* primarily to reduction in STF innervation concomitant with the reduction in size of this muscle, because this is the case in *Emerita*, where the STF (ME) muscle is innervated by a single motoneuron (Paul, 1971b). Analogous reductions in numbers of motoneurons correlated with hypotrophy of muscles have occurred in the abdomen of pagurids (Chapple, 1977; see also Mittenthal and Wine, 1978), whereas the number has remained constant for the homologous muscles of similar size in macrurans (Kahan, 1971). The PTF (VM) muscle in *Emerita* is innervated by five motoneurons (Paul, 1971b), two fewer than in crayfish; from some positions and neurite branching patterns of the R6 motoneurons it appears that in addition to its motor giant one of the peripheral inhibitory neurons has been lost. We think this may also be the case in *Munida* and *Blepharipoda*. The uncertainty in the latter two animals stems from multiple branching of the nerves to both STF and PTF which reduces the confidence with which we could assign motoneurons backfilled from individual nervelets to particular muscles. In conclusion, Table III should be considered as setting forth a series of specific hypotheses about telson axial neuromusculature that can be tested experimentally by comparing physiological properties of individual motoneurons with those of their homologs in crayfish (Dumont and Wine, 1983, in prep.; Larimer and Kennedy, 1969a; see also Kahan, 1971; Chapple, 1977; Mittenthal and Wine, 1978; Sillar and Heitler, 1982).

#### DISCUSSION

We have described the organization of the neuromusculature in the telsons of decapod Crustacea. We use this plan to suggest homologies between individual muscles, nerve roots, and motoneurons in three macrurans and three anomurans (Table II; Figs. 4, 5). The most significant functional difference in the telson musculature of these anomurans compared to macrurans is the freedom of the appendage (TU) muscles from actions of the axial muscular system. This difference arose by two definitive peripheral changes: elimination of mechanical coupling between flexor and TU muscles and the elimination of the TU tendon, so that the TU muscle fibers in anomurans arise directly from the dorsal telson. Our results also reveal some specific neural changes that accompanied the evolution of the anomuran tailfans but that are not, apparently, correlated with any change in mode of swimming (tailflipping).

#### *Neural correlates of the emancipation of the TU muscles from the axial muscular system*

*Loss of giant interneurons and motor giants.* Macrurans have one or two pairs of giant interneurons (the medial and lateral giant neurons, MG and LG) that mediate in part rapid flexions of the abdomen and tailfan (Bullock and Horridge, 1965; Wine and Krasne, 1982). The pair of giant interneurons in *Callinassa* (and *Upogebia*) is the homolog of the MGs in crayfish (Turner, 1950). The loss of the LGs in these two macrurans was probably secondary to adoption of their burrowing habit. Wine and Krasne (1982) summarize evidence from the cellular organization of crayfish escape behavior that suggests evolution of the giant systems (interneurons, motor giants, and segmental giants) from non-giant neurons. We assume that the giant interneurons were present in the macrurans from whom anomurans evolved. They may have been

present in the earliest decapods, considering that (1) their putative homologs occur in a primitive eumalacostracan (Silvey and Wilson, 1979), (2) the abdomens and tailfans of Devonian fossil and modern macrurans are externally very similar (Schram *et al.*, 1978), and (3) the likelihood that decapods evolved in a near-shore marine habitat (Schram, 1981) in which, presumably, the different forms of rapid, escape tailflips would have been as adaptive as they appear to be today.

Increased autonomy of the enlarged TU muscles in anomurans is correlated with the absence of the giant interneurons (Paul, 1971a; Sillar and Heitler, 1982; Paul and Then, unpub.). Concurrent with the demise of the giant interneurons may have been the loss of the specialized fast flexor motoneurons, the motor giants (MoG) in G6. Our R6 motoneuron counts and morphological data suggest that the one MoG innervating PTF is present in G6 of *Upogebia*, but not in G6 of *Emerita* or either of the tailflipping anomurans, *Munida* or *Blepharipoda* (Table III; Fig. 5). Sillar and Heitler (1982) proposed that an "unspecialized" fast flexor motoneuron in the mid-abdominal ganglia of *Galathea strigosa* (Galatheidae) is homologous to crayfish's MoG. This suggests that members of the serial set of MoGs may have fared differently in the evolution of galatheid anomurans, those in G6 having been lost (one with the demise of VTF, the other reducing PTF's innervation), while those in other abdominal ganglia were retained. Alternatively, an unspecialized MoG may be retained in G6 and one of the fast flexor motoneurons lost. Physiological descriptions of the R6 motoneurons in anomurans to compare with their crayfish homologs (Dumont and Wine, 1983, in prep.) are needed to distinguish between these possibilities.

*Uropod stretch receptor*. The uropod coxal receptor (SR; Fig. 3A<sub>2</sub>-C<sub>2</sub>) has been described previously in *Emerita analoga* (Paul, 1971c, 1972) and in *Galathea strigosa* (Maitland *et al.*, 1982). The latter authors mistook the articulation between telson and segment 6 for an "anterior mid-dorsal hinge in the middle of the 6th abdominal segment" and, therefore, erroneously described the SR's dorsal attachment as being to the middle of segment 6 instead of to the anterior telson.

Serially homologous SRs, innervated by receptor neurons with central somata, occur at the base of segmental appendages in the head (Pasztor, 1969; Pasztor and Bush, 1983), the thorax (Alexandrowicz and Whitear, 1957; Blight and Llinas, 1980), and the abdomen (Heitler, 1982); such sensory structures might have been associated with each of the appendages in primitive crustaceans, including the terminal pair, which probably were more swimmeret- than uropod-like (*cf.*, *e.g.*, modern Nebaleidae). They would then have been lost from the uropods in the subsequent evolution of the eumalacostracan tailfan. Among decapods, uropod SRs occur in the galatheids and albuneids, anomurans that swim by tailflipping in a manner similar to their macruran ancestors (Paul, 1981b, unpub.; Maitland *et al.*, 1982; this study).

The coxal SRs reflexly excite motoneurons in dissected animals, but in most cases little is known about their role in behavior (Blight and Llinas, 1980; Heitler, 1982; Maitland *et al.*, 1982). In *Emerita* they mediate a "complete" resistance reflex that includes reciprocal excitation and inhibition of both excitatory and peripheral inhibitory motoneurons of the PS (PTU) and RS muscles, and they also modulate VM (PTF) motoneuron activity (Paul, 1971c, 1972, unpub.). One function of this reflex is to coordinate uropod power strokes (PTU motoneuron bursts) in the 'treading water' behavior of this sand crab (Paul, 1976). When more is known about the role of the uropod SRs in tailflipping anomurans (Maitland *et al.*, 1982), comparison with *Emerita*'s nonspiking SRs may reveal what specific advantage analog signaling conveys that counterbalances the metabolic cost of developing and maintaining such large neurons (Pearson, 1979; Shepherd, 1981).

*From tailflipping to swimming with the uropods*

This and other studies (Larimer and Kennedy, 1969; Paul, 1971a, b, 1972, 1981a, b; Maitland *et al.*, 1982; Dumont and Wine, 1983, in prep.) provide enough comparable data on the tailfans of different decapods to suggest an evolutionary history of the telson neuromusculature in *Emerita* from the macruran plan. Although the rami of macruran uropods can be flared horizontally by the action of muscles located within the propodite, movement of the appendage relative to the body is quite restricted. Correlated with greater uropod mobility in galatheids and albuneids are reduction of axial flexor muscles, hypertrophy of the TU muscles, and the appearance of the uropod SR. Mechanical linkage between appendage and axial muscles in the telson is gone in both families, but in galatheids the VR muscle in segment 6 is partially fused with the deep-lying fast flexors as it is in macrurans (Fig. 3A). In albuneids, potentially greater independence of the uropods from axial movements is made possible by loss of the VR muscle and addition of a 'new' appendage muscle in the telson (the RS muscle) to elevate the uropod (Fig. 3B; Paul, 1981b). The absence of RS in galatheids, which otherwise albuneids resemble in both telson neuromusculature and tailflipping behavior, would appear to confirm that RS is a 'new' muscle, peculiar to sand crabs (Paul, 1981b). Finally, correlated with the transition from tailflipping to the hippid behavior of swimming with the uropods were three kinds of changes in the telson, all involving muscular and neural components present in the tailflipping, albuneid sand crabs: (1) the insertion of PTF, the principal remaining axial muscle, was moved from axis to uropod; (2) two appendage muscles and their motoneurons experienced tremendous hypertrophy: an ancestral macruran muscle, PTU, to become the uropod power-stroke muscle, and the sand crabs' new RS muscle (Fig. 3; Paul, 1981b); and (3) the physiology of the uropod stretch receptor neurons changed from digital to analog signaling (Paul, 1972, unpub., Maitland *et al.*, 1982).

Paul (1981b) had suggested possible derivation of *Emerita*'s power-stroke (PS = PTU) muscle from the macruran axial muscle, PTF, with a change in exit of the two PS motoneurons from R6 to R2. Having now identified all of the homologs between the telson muscles in *Emerita* and macrurans (Table II) and located their motoneurons in G6 (Fig. 5), we can discard this hypothesis. The resemblance between crayfish's PTF muscle and *Emerita*'s PTU muscle (compare Fig. 1A<sub>1</sub> and Fig. 3C<sub>2</sub>) is clearly an example of convergent evolution, the result of the need for both muscles to be oriented longitudinally because the swimming strokes they mediate are parallel to the long axis of the body—the flexion-extension of the abdomen in the ancestral behavior of tailflipping and the uropod stroke in the hippid mode of swimming with the uropods. The axons exit through the appropriate root to innervate axial and appendage respectively. Thus the conservation of root of exit of motoneurons in mid-body ganglia (Mittenthal and Wine, 1978) appears to be true for the terminal ganglion as well.

The cumulative observations leading to this scenario reinforce the suggestion that swimming with the uropods evolved directly from non-giant mediated tailflipping, and that homologies between elements of the neuronal circuitries mediating each of these two behaviors must exist (Paul, 1971a, 1979, 1981a, b). Both behaviors rely on central generation of the reciprocal pattern of motor activity for power and recovery phases of the swimming stroke (Paul, 1979; Reichert *et al.*, 1981). In *Emerita*, this pattern is expressed by centrally generated bursting of both PTF and PTU motoneurons. Comparable recordings of the motor pattern in crayfish have not been made because it is not spontaneously expressed by the isolated nervous system and a way of eliciting

it has not yet been found. However, neurites of the PTU motoneurons in *Procambarus* (Paul, unpub.) and their homologs, the PS motoneurons, in *Emerita* (Paul, 1981b) project rostrally in G6 to comparable regions of large, dorsal cord axons (DCA) entering from the 5–6 connective. In *Procambarus*, some of these DCAs belong to the non-giant circuitry for tailflipping (Kramer *et al.*, 1981a, b; Wine and Krasne, 1982; Kramer and Krasne, 1984), but nothing is yet known about activity of the TU muscles during this behavior. These comparisons raise two questions that are particularly relevant to the evolution of the hippid swimming behavior: are crayfish PTU motoneurons included in the centrally generated motor pattern for repetitive tailflipping as their central anatomy might suggest? And, are the DCAs in *Emerita* part of the circuit for the uropod central motor program, and, therefore, candidate homologs of specific DCAs in crayfish? If both answers are affirmative, then the connections between DCAs and the PTU (as well as the PTF) motoneurons are potential loci for neural changes incurred during the evolution of the new hippid swimming behavior.

### *General Discussion*

Since the telson is not a somite, with appendages and a ganglion of its own, and, in fact, is little more than a skeletal tailpiece in primitive Crustacea, it is not obvious how in decapods it came to house a neuromusculature nearly as rich and diverse as is present in the body segments. We suggest that the appendage musculature in decapod telsons is ontophyletically neuromusculature of abdominal segment 7. Without development of a seventh abdominal segment in decapods, the terminal ganglion became a fusion of the sixth and seventh abdominal ganglia (plus a terminal cell cluster) (Bullock and Horridge, 1965; Dumont and Wine, in prep.), and muscles of primordial segment 7 that were retained came to be located in the anterior part of the telson.

In a penaeid (suborder Dendrobranchiata), whose morphology is considered to represent a “generalized decapod condition,” Young (1959) described protopodite remotor and rotator muscles that appear to be homologs of the TU muscles in the suborder Pleocyemata. The main difference is that their dorsal origin is from connective tissue in the plane of articulation between segment 6 and telson, a position that suggests they could be derivatives of the primordial seventh abdominal segment. They are unlikely to be segment 6 appendage muscles because these are accounted for by the rotator and remotor muscles (Figs. 1, 3). This would make the TU muscles the serial homologs of the dorsal rotator muscles in segment 6.

When the uropods of anomurans acquired greater mobility than in macrurans, additional structures characteristic of segmental appendages were expressed: the SRs with central somata, and, in sand crabs, uropod remotor (=RS) muscles in the telson. In an earlier study Paul (1981b) surmised that the RS muscle had been derived from the remotor muscles (=LR) in the 6th segment on the basis of the innervations, and similarities in positions and morphologies of the motoneurons innervating these two muscles. A reinterpretation of these features is that they reflect serial homology of the RS and the 6th segment remotor neuromusculature, the RS muscle being segment 7 remotor expressed in the telson. Thus, the “new” muscle and its motoneurons in the sand crab telsons, as well as the phylogenetically older TU muscles, would be products of an ontogenetic potential for a 7th abdominal segment the development of which was repressed in decapod evolution. These ideas are highly speculative, and developmental studies of G6 and telson in these species would help clarify the relationships among the neuromuscular components of their tailfans.



Two other components of the tailfan's neural and muscular systems are also thought to be derivatives of both 6th and 7th segments: the fast flexor neuromusculature in the telson (Dumont and Wine, 1983, in prep.), and the uropod SR in *Emerita* which has four nonspiking sensory neurons (Paul, 1972) compared to the two nonspiking neurons in the swimmeret SR (Heitler, 1982). It appears, therefore, that in decapods the only neuromusculature in the telson with no rostral homologs may be the AT muscle and its single excitatory motoneuron (Dumont and Wine, in prep.). This muscle and its motoneuron have been lost in anomurans.

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